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Mirror neurons and intention understanding:

Dissociating the contribution of object type and intention to mirror responses  
using electromyography

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### Abstract

Since their discovery in the monkey and human brain, mirror neurons have been claimed to play a key role in understanding others' intentions. For example, "action-constrained" mirror neurons in inferior parietal lobule fire when the monkey observes a grasping movement that is followed by an eating action, but not when it is followed by a placing action. It is claimed these responses enable the monkey to predict the intentions of the actor. These findings have been replicated in human observers by recording electromyography responses of the mouth-opening mylohyoid muscle during action observation. Mylohyoid muscle activity was greater during the observation of actions performed with the intention to eat than of actions performed with the intention to place, again suggesting an ability to predict the actor's intentions. However, in previous studies, intention was confounded with object type (food for eating actions, non-food for placing actions). We therefore used electromyography to measure mylohyoid activity in participants observing eating and placing actions. Unlike previous studies, we used a design in which each object (food, non-food) could be both eaten and placed, and thus participants could not predict the actor's intention at the onset of the action. Greater mylohyoid activity was found for the observation of actions performed on food objects, irrespective of intention: indicating that the object type, not the actor's intention, drives the mirror response. This result suggests that observers' motor responses during action observation reflect the presence of a particular object, rather than the actor's underlying intentions.

*Keywords:* mirror neuron, electromyography, EMG, mylohyoid, action observation, action understanding, intention understanding

## Mirror neurons and intention understanding:

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Understanding others' intentions from the observation of their actions has often been claimed to be one of the possible functions of 'mirror' neurons – a specific class of visuomotor neurons that discharge both when performing a given motor act and when observing the same or a similar act performed by a conspecific. These neurons were first discovered in area F5 of the ventral premotor cortex (di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996) and in the inferior parietal lobule (Fogassi, Ferrari, Gesierich, Rozzi, Chersi, & Rizzolatti, 2005; Rozzi, Ferrari, Bonini, Rizzolatti, & Fogassi, 2008) of the macaque brain. Although to date only one study has employed single cell recordings to provide direct evidence of mirror neurons in the human brain (Mukamel, Ekstrom, Kaplan, Iacoboni, & Fried, 2010), a substantial number of studies using indirect techniques including neuroimaging and transcranial magnetic stimulation suggest that a mirror mechanism (i.e. the activation of the same motor cortical areas during action observation and action execution) operates also in the human brain (see Molenberghs, Cunnington, & Mattingley, 2012 for a review).

The distinctive feature of mirror neurons is that they match an observed action with one's own motor representation of that action: perceiving a motor act activates the same motor network required by the observer to execute that action him- or herself (Rizzolatti & Sinigaglia, 2008). It has been claimed that, as a result of the overlap between brain areas activated during perception and during execution, the observer is able to directly and immediately understand others' actions (*what* they are doing) and to attribute to them

intentions (*why* they are doing it), without the mediation of other cognitive or inferential processes (Rizzolatti & Sinigaglia, 2007; Rizzolatti & Fogassi, 2014).

It has been suggested that the ability to infer intentions from actions is a component process contributing to a more general concept that has broadly been termed ‘action understanding’ (Hamilton & Grafton, 2008). The component abilities within this broader concept comprise: detecting lower-level *action kinematics* (e.g. differences in hand shape between a precision grip and a whole hand grip); understanding *action goals* (i.e. the immediate outcome of an action, like pressing a switch); and understanding *intentions* (i.e. the higher-order mental state or motivation generating that action, like pressing a switch in order to turn the light on rather than off). The term ‘intention understanding’ has most often been used, in the mirror neuron literature, in this latter sense (i.e. to refer to the motivation producing a certain action), and mirror neurons have been claimed to subserve the ability to identify an actor’s underlying motivation (Rizzolatti & Sinigaglia, 2007; Rizzolatti & Fogassi, 2014).

In assessing this claim, one must first establish whether, in principle, it is possible to determine another’s intention from the mere observation of their actions. Existing data support this possibility. It has been demonstrated, for example, that actions performed with different intentions have reliable perceptual differences; an actor’s intention can modulate the kinematics of the performed action, even when, for example, reach-to-grasp movements are performed on the same object (Marteniuk, MacKenzie, Jeannerod, Athenes, & Dugas, 1987; see also Schuboe, Maldonado, Stork, & Beetz, 2008). In a recent study, Naish and colleagues (2013) demonstrated that kinematic profiles of reach-to-grasp movements systematically differed depending on whether the intention of the actor was to place an object into a container or to bring it to the mouth. Furthermore, Cavallo et al. (2016) provided preliminary evidence that not only is intention information available in action kinematics, but this

information can be effectively perceived and exploited by the observer in order to infer the actor's intentions (for a more detailed discussion of the literature on this subject see Catmur, 2015).

The claim that mirror neurons support such a process of intention understanding is largely based on data from two particularly influential studies on macaques and humans, which utilised single-unit and electromyographic techniques respectively to measure motor responses during the observation of actions performed with different intentions. However, in both studies, the experimental design employed by the authors did not fully control for the effects of confounding variables, such as the influence of the different types of objects on which the actions were performed, or of other contextual cues available in the experimental setting. Fogassi et al. (2005) carried out single-cell recording in macaque inferior parietal lobe neurons while the macaques performed and observed grasping actions as part of a sequence involving either an eating or a placing intention. In the motor performance task, the monkey grasped a piece of food in order to eat it, or grasped a non-food object in order to place it into a container. Similarly, during the observation task, the monkey observed the same actions performed by an experimenter. Out of all studied neurons in both the performance ( $n=165$ ) and observation tasks ( $n=41$ ), 64.2% and 75.6%, respectively, showed intention selectivity: the firing rate of the neurons was influenced by the intention (eating, placing) of the performed or observed grasping action. The authors concluded that during action observation, neurons involved in action performance fire according to the observed actor's intention, and that this response allows the monkey to understand the actor's intention. However, in these tasks, the intention was confounded with the object type (food for eating intentions, non-food for placing intentions), and therefore the intention-selective response could be driven by the object type, rather than the actor's intention. That is, the presence of a food object could trigger neurons coding for grasping-to-eat actions rather than

neurons coding for grasping-to-place actions. The authors therefore introduced a third condition in which the experimenter grasped a piece of food in order to place it into a container. In this condition, the firing rate remained the same regardless of the object grasped (i.e. whether it was a non-food object or a piece of food). However, across the three observation conditions, a container was present during actions performed with a placing intention, but not during actions performed with an eating intention, meaning that the presence of a container provided a contextual cue to the actor's intention.

Building on the results of Fogassi et al. (2005), Cattaneo and colleagues (2007) used a similar design to investigate the mechanism underlying intention understanding in humans. They recorded electromyographic (EMG) activity of the mouth-opening mylohyoid muscle in eight typically developing children and in seven high-functioning children with autism, while they performed and observed grasping actions with eating versus placing intentions. Although all children showed greater mylohyoid activity when performing actions with an eating versus a placing intention, during the observation condition this pattern differed between the two groups: Typically developing children, but not children with autism, showed greater mylohyoid activity when observing someone else reaching for food to eat it, rather than reaching for a non-food object to place it into a container. These results have been interpreted as evidence, in humans, for mirror neurons that respond to observed actions as a function of the actor's intention; and as evidence for dysfunction of such mirror neurons in children with autism.

This latter claim has been disputed on various grounds, most specifically by Pascolo and Cattarinussi (2012). Under more controlled testing conditions, Pascolo and Cattarinussi demonstrated that, during action performance, the distance between the participant and the food may have played a key role in the difference in mylohyoid activation between the typically developing children and the children with autism. They also provided data

suggesting that potential attentional disturbance factors, such as the presence of several experimenters during the tasks, might have influenced the results.

Here we focus on the first claim, regarding whether Cattaneo et al. (2007)'s results provide evidence for intention-selective mirror neuron responses. As in Fogassi et al. (2005), Cattaneo et al.'s experiment confounded the actor's intention (eating, placing) with the object type (food, non-food). When observing someone reaching for a food rather than a non-food object, the observer can predict that food is going to be eaten, rather than placed. In order to infer intentions, observers may extrapolate from the context in which actions are performed. Objects can be considered contextual cues to the likely actions that will be performed upon them, due to prior associations (e.g. food is usually associated with the action of eating). The presence of this clear contextual cue (food) could therefore explain the differential muscle activation in the two intention conditions.

To overcome this issue, Cattaneo et al. (2007) included a third condition in which participants observed an actor grasp a piece of paper and place it in the mouth. Greater mylohyoid activity was found when observing the actor reaching for the paper (with the intention to 'eat' it), than when reaching for another object to place it. However, this experiment did not control fully for the previous confound of intention with object type because it employed two different non-food objects, a piece of paper which was 'eaten' and a small toy which was placed in a container. Hence, when observing actions performed on the paper, participants could predict that this was going to be placed into the mouth, whereas when they saw actions performed on the toy, they could predict that this was going to be placed in the container.

This summary demonstrates that when investigating intention understanding, in order to control fully for the effect of object type, an experimental design is required in which each object type (food, non-food) can be acted upon with each intention (eating, placing). Such a



design ensures that the observer cannot predict the actor's intention from either the object identity, or from other contextual cues such as the presence or absence of a container.

The present study employed such a design to investigate whether mirror responses (i.e. motor responses during observation of others' actions) have the potential to contribute to determining intentions from observed actions. Like Cattaneo et al. (2007), we employed EMG to measure mylohyoid muscle activity. The use of facial EMG to infer the relative activity of the motor representations associated with the measured musculature is common in both the mirror neuron and the broader social neuroscience literatures (Cattaneo et al., 2007; Pascolo & Cattarinussi, 2012; Oberman, Winkielman, & Ramachandran, 2007; Davis, Winkielman, & Coulson, 2017). For example, observing someone else performing arm actions (Berger & Hadley, 1975) and non-emotional face movements (Moody & McIntosh, 2011) elicits in the observer an increase of activity in the same muscles involved in the actions observed. Interestingly, one study that used both facial EMG and functional magnetic resonance imaging to investigate the role of mirror neurons in automatic facial mimicry, found a significant correlation between the activity of facial muscles and the BOLD response in several mirror neuron areas (Likowski, Mühlberger, Gerdes, Wieser, Pauli, & Weyers, 2012).

Using an action observation task related to those of Fogassi et al. (2005) and Cattaneo et al. (2007), we recorded activity of the mylohyoid muscle while participants watched an actor reaching to grasp one of two objects (a food object and a non-food object). On each trial, the object could be 'eaten' (for the non-food object, this meant it was placed into the mouth) or placed into a container. Mylohyoid activity was recorded during both the reaching and bringing phases of the observed movement (i.e. before and after the contact between the actor's hand and the object), to facilitate comparison with Cattaneo et al.'s results in which greater mylohyoid activity was found for the observation of 'eat' than of 'place' intentions even during the reaching phase of the observed movement. If mirror

responses contribute to understanding intentions, then we should observe greater activity of the mylohyoid muscle (involved in mouth opening) during the observation of actions performed with the intention to eat, rather than during actions performed with the intention to place, irrespective of the object type. Furthermore, this effect should already be present during the reaching phase of the observed movement. In contrast, if the object type drives the mirror response then greater mylohyoid activity should be found for food objects irrespective of the actor's intention. Since the object type is a contextual cue that is visible to participants from the onset of each trial, this effect should also be present during the reaching phase of the observed movement.

## **Method**

### **Participants**

Thirty volunteers (23 female, 7 male,  $M_{age} = 25.57$  years, age range = 20-40 years) were recruited via the University of Surrey research participant website. The study was given a favourable ethical opinion from the University of Surrey Ethics Committee. All participants gave informed consent prior to participation and received a small financial compensation for their time. This sample size provides over 85% power to detect a medium effect size at an alpha level of .05, and is over three times the sample size in the neurotypical participant group of Cattaneo et al. (2007) in which a significant effect of intention was observed.

### **Design**

Participants were shown videos of eating and placing actions while electromyographic EMG activity of the mouth-opening mylohyoid muscle was measured. The adult male in each video reached out to grasp either some food or a non-food object from a box and then either ate it (for the non-food object this consisted of holding it in the mouth) or placed it into another container at his shoulder.

The experiment used a 2 x 2 x 2 within-subject design, wherein the independent variables were the intention (eating, placing), the object type (food, non-food) and the action phase (reaching: when the actor reached towards the object, and bringing: when he brought it to the mouth/container), with normalised EMG values of the mylohyoid muscle as the outcome measure. Since each object (food, non-food) could be both eaten and placed, the observer could not predict the actor's intention at the onset of the action.

### **Stimuli**

Four different types of video, lasting approximately 13 seconds each, were recorded. Each video started with a man sitting behind a desk. An empty box was located in front of him, a second box containing food (raisins) and a non-food object (a small plastic toy) was placed at the left of the desk (from the participant's perspective), while a third empty box was located on a shelf at the man's left shoulder level (on his right from the participant's perspective). An experimenter took one of the objects (either food or non-food) from the left box and placed it into the central box, then the actor in the video, (the same actor was used for all videos), reached for and grasped the object and brought it towards him, whereupon he either ate it (EatFood condition / EatNon-food condition) or placed it (PlaceFood condition / PlaceNon-food condition) into the container at his shoulder level. In order to control for any potential differences in the behaviour of the actor across the conditions, two different videos for each condition were recorded. Stimuli were presented using E-Prime 2.0 software (Psychology Software Tools, Pittsburgh, PA).

### **Procedure**

Before EMG electrodes were placed, participants prepared their skin with an alcohol solution. Electrolytic conducting gel was applied to the electrodes, which were then secured with surgical tape. Participants were seated in front of the computer screen, and they were told to pay close attention while watching the videos. The experiment comprised two blocks

of 40 videos (10 per condition) presented in a random order. Since we recorded two different videos for each condition, each video was randomly presented 5 times. A rest period was allowed between the blocks, and each video was preceded and followed by a fixation cross presented for 1,000ms. The video session lasted approximately 20 minutes.

**Electromyography recording and pre-processing.** The activity of the mylohyoid muscle was recorded using 8mm diameter Ag/AgCl surface electrodes (E272, EasyCap GmbH, Woerthsee-Ettersschlag, Germany) placed under the chin and symmetrically to the midline, one serving as the active electrode and the other one as reference. The ground was placed over the participant's jawbone. The signal was amplified (1,000x), sampled (1 kHz), band-pass filtered (30-500Hz), and stored for off-line analysis.

EMG activity was measured for 2000ms before and 2000ms after the time point at which the actor grasped the object. EMG values were rectified, normalised to each participant's mean EMG response to reduce between-participant variability (Halaki & Ginn, 2012) and divided into 100ms time intervals (as in Cattaneo et al., 2007). We obtained, thus, 40 time intervals for each condition. Artefact removal (see below) was performed at this stage. Following artefact removal, within each condition (EatFood, EatNon-food, PlaceFood, PlaceNon-food) mean normalized EMG values were calculated for the 20 intervals before the grasp and for the 20 intervals after the grasp in order to split the action into two phases: when the actor reached towards the object (Reach), and when he brought it into the mouth/container (Bring).

## Results

Inspection of the data revealed the presence of occasional artefacts (extremely high EMG values) presumably due to overt muscle activity such as swallowing or other movements during the course of the experiment. Most participants had at least one artefact in at least one of the 100ms time intervals for at least one of the four video types. Extreme

outlying values, (greater than 3 times the interquartile range; 4.8% of all datapoints) were therefore Winsorized, being replaced with the next-closest non-outlying score. Winsorizing rather than data exclusion was used because Winsorized data are considered more robust than trimmed data (Tukey, 1962). One participant's data were excluded from subsequent analysis at this point since they were found to be an outlier for the majority of time intervals for all video types. Twenty-nine participants (22 female, 7 male,  $M_{\text{age}} = 25.69$ , age range = 20-40) were therefore included in the final analysis.

Table 1 shows mean normalized EMG values with standard deviations for the eight variables. Recall that, if participants are able to anticipate the actor's intentions on the basis of his actions, EMG activity in the mylohyoid muscle should be higher in the Eat than the Place action condition, regardless of the object type; and they should show this pattern of results already in the Reach phase. Alternatively, if the ability to anticipate the actor's intentions is driven by the object type, EMG values should be higher in the Food than the Non-food condition, and again this pattern of results should already be present in the Reach phase.

Table 1 about here

A 2 x 2 x 2 repeated measure analysis of variance (ANOVA) was performed with dependent variable of normalized EMG values and independent variables of intention (Eat, Place), object type (Food, Non-food) and phase (Reach, Bring). The ANOVA revealed a main effect of object type, with significantly greater activity of the mylohyoid muscle when participants observed actions performed with food than with non-food objects,  $F(1, 28) = 5.061$ ,  $p = .033$ ,  $\eta^2_p = .153$ . A significant main effect of phase was also observed,  $F(1, 28) = 7.136$ ,  $p = .012$ ,  $\eta^2_p = .203$ , with a greater mylohyoid activity during the observation of the reaching phase of the action rather than the bringing phase. However, there was no interaction between the phase and any other factor. Finally, a significant interaction was

found between object type and intention,  $F(1, 28) = 6.232, p = .019, \eta^2_p = .182$ . Follow-up  $t$ -tests indicated that this effect was due to a significant difference in EMG activity during the observation of placing actions, with lower EMG activity during the observation of placing actions performed with a non-food object than with a food object,  $t(28) = 2.827, p = 0.009, d = 0.914$ , whereas mylohyoid activity did not significantly differ between object types when observing eating actions; and did not differ as a function of the actor's intention for either the food or the non-food object. This interaction is illustrated in Figure 1.

Figure 1 about here

In order further to investigate the main effect of phase, and to facilitate comparison with previous studies (e.g. Cattaneo et al., 2007), a follow-up analysis was run which enabled a more fine-grained investigation of the timecourse of the effects. In this analysis, the factor of phase was replaced by one of timepoint, with 40 levels (20 intervals before and 20 after the grasp). A  $2 \times 2 \times 40$  repeated measure ANOVA was run with dependent variable of normalized EMG values and independent variables of intention (Eat, Place), object type (Food, Non-food) and timepoint (20 intervals before and 20 intervals after the grasp). As in the first analysis, the ANOVA revealed a main effect of object type, with significantly greater activity of the mylohyoid muscle when participants observed actions performed with food than with non-food objects,  $F(1, 28) = 5.072, p = .032, \eta^2_p = .153$ . As with phase in the first analysis, we observed a significant main effect of timepoint,  $F(39, 1092) = 1.990, p < .001, \eta^2_p = .066$ , with rather stable mylohyoid activity from timepoint 1 to timepoint 20 (equivalent to the reaching phase) and with a substantial decline from timepoint 20 (when the actor grasped the object) to timepoint 33 (towards the end of the bringing phase). Once again, a significant interaction was found between object type and intention,  $F(1, 28) = 6.249, p = .019, \eta^2_p = .182$ . Finally, this follow-up analysis also revealed a significant interaction between object type and timepoint,  $F(39, 1092) = 1.684, p = .006, \eta^2_p = .057$ . This interaction

is illustrated in Figure 2, and it suggests that, irrespective of the intention, mylohyoid activity was relatively stable across timepoints when participants observed actions performed with food objects, but it decreased – particularly after the grasp – when they observed actions performed with a non-food object.

Figure 2 about here

These results suggest that the object type, rather than the intention, may drive mirror responses, since participants showed increased mylohyoid activity when observing actions performed with food. The initial analysis indicated that this was broadly the case across the two general action phases (reaching or bringing), whereas the follow-up analysis indicated that the main effect of object type was driven by a difference in mylohyoid activity during the end of the reaching phase and throughout the bringing phase; however, given the lack of an interaction between object type and action phase in the initial analysis, this second finding should be considered only preliminary.

### **Discussion**

Our study aimed to use electromyography to investigate the role of mirror neurons in intention understanding. We measured the mirror response (i.e. the motor response during action observation) in the mylohyoid muscle (involved in mouth opening) to the observation of actions performed with either eating or placing intentions, on food and non-food objects. In contrast to the results obtained by Cattaneo et al. (2007), we did not find evidence that mirror responses distinguish between observed actions on the basis of the actor's intentions; rather, we found that, when object type and intention are not confounded, mirror responses are driven by the identity of the object being grasped, not by the actor's intention. Participants showed increased mylohyoid activity when observing actions performed on food than on non-food objects, regardless of the action phase (reaching or bringing). This result confirms that the object type, rather than the intention, drives mirror responses. Since food is

usually associated with eating actions, it elicited a higher response in the mylohyoid muscle than the non-food object, regardless of whether the actor's intention was to eat or to place it. Our data therefore do not support the hypothesis that mirror responses are involved in intention understanding.

Interestingly, as well as the main effect of object type, an interaction was found between object type and intention. Participants showed no difference in mylohyoid activity as a function of the actor's intention within each object type. In particular, they showed no difference between the observation of eating and placing actions performed with food objects, emphasising that the actor's intentions did not influence the mirror response to actions performed with food objects when the object type was kept constant. Furthermore, consistent with the main effect of object type, when participants observed placing actions performed with non-food objects, mylohyoid activity was significantly lower than when observing placing actions performed with food objects. The interaction between object type and intention was therefore driven by the relatively greater mylohyoid activity in the condition in which the actor grasped a non-food object and brought it to his mouth to 'eat' it, compared to the condition in which he placed it in a container. This result is not consistent with a role of mirror responses in understanding others' intentions, since in that case a main effect of intention on mylohyoid response should have been observed, with greater mylohyoid response for the eating intention regardless of the object type. Rather, it suggests that in the non-food 'eating' condition, participants may have learned that the non-food object could be placed into the mouth, resulting in an increase in mylohyoid activity when observing 'eating' of a non-food object.

If muscle activity during action observation reflects the identity of the observed object, rather than the actor's underlying intention, this suggests that mirror responses (motor responses to observed actions) do not, alone, support intention understanding. Our data



therefore inform the current debate on the possible mechanisms underlying intention understanding (e.g. Catmur, 2015; Tidoni & Candidi, 2016) by indicating that previous studies, in which intention and object type were confounded (e.g. Fogassi et al., 2005; Cattaneo et al., 2007), can no longer be taken as evidence for mirror neuron contributions to intention understanding. The current results therefore suggest that future studies need to investigate the contribution of mirror neurons to intention understanding using stimuli in which the object type is kept constant while the intention is manipulated (see Cavallo et al., 2016 for an example of a task illustrating the feasibility of this approach).

The current data also have implications for the so-called ‘broken mirror’ theory of autism (Oberman & Ramachandran, 2007). The results of Cattaneo et al. (2007) have been interpreted as supporting that theory because they were considered to demonstrate a dysfunction in the ability to understand others’ intentions in children with autism. If, as our data suggest, mirror responses do not reflect the actor’s intention, then the results observed by Cattaneo et al. cannot be interpreted as demonstrating a deficit in intention understanding. It is possible that, in Cattaneo et al.’s study, the lack of a difference in mylohyoid activity in children with autism between observation of grasp-food-to-eat and grasp-non-food-to-place actions could be due to impairments in other abilities required by the task, such as attentional and inferential demands. For example, the children with autism may have paid less attention to the food objects than to the non-food objects; or they may have paid sufficient attention to the food objects, but due to reduced attention to social stimuli (e.g. Bird et al., 2006) during development, they may have had insufficient previous experience to allow them to associate social stimuli (the experimenter’s actions) with their own motor programs (Heyes, 2001).

One limitation of our study is that we employed EMG as an indirect method to infer mirror responses (i.e. activation of the mylohyoid muscle during action observation), rather than measuring neural responses more directly. EMG activity cannot always and invariantly

be linked to specific information processes or psychological states (Fridlund & Caccioppo, 1986). However, the highly-controlled nature of the stimuli used in this study allows us to infer that any systematic changes in EMG activity are due to the independent variables. Furthermore, as we discussed above, previous studies used EMG to infer mirror responses (Cattaneo et al., 2007; Pascolo & Cattarinussi, 2012; Likowski et al., 2012) and, more generally, to study the association between muscle responses and the activity of their matching motor representations (Oberman et al., 2007; Davis et al., 2017). Future studies could however use more direct measures of mirror responses, such as motor-evoked potentials, to address this issue.

Another limitation of our study is that we used 2D videos as a stimulus to elicit mylohyoid responses, and one could argue that observing 2D actions does not reflect the complexity of observing real-life actions. This choice was driven by the aim of replicating previous experiments under more controlled conditions. By using videos, the length of the reaching and bringing movements, and of the overall action, was kept constant across all conditions. Furthermore, the video stimulation allowed us to control for possible distractions that could have influenced participants' muscle response during the task, such as unintentional movements or facial expressions of the actor while he was performing the movements. It should also be noted that 2D pictures and videos are often used in the mirror neuron literature, including in studies investigating their involvement in action understanding (e.g. Iacoboni et al., 2005; Pobric & Hamilton, 2006; de Lange, Spronk, Willems, Toni, & Bekkering, 2008).

In conclusion, the present data suggest that mirror responses during action observation are sensitive to the identity of the object that is being grasped, rather than to the intention of the actor. Previous studies purporting to show a role of mirror neurons in understanding others' intentions may have confounded intention with object type.

These data do not support the hypothesis that mirror neurons are the neural substrate for understanding others' intentions, and they therefore suggest that other possible candidates, such as networks of brain areas underlying inferential processing, should be investigated by future research.

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## Tables

Table 1

*Mean and standard deviation of the normalized electromyography values recorded from the mylohyoid muscle during the two phases of each of the four observation conditions*

<b>Condition - Phase</b>	<b>M</b>	<b>SD</b>
Eat Food – Reach phase	1.00	0.11
Eat Food – Bring phase	0.98	0.10
Eat Non-food – Reach phase	1.01	0.10
Eat Non-food – Bring phase	0.97	0.11
Place Food – Reach phase	1.05	0.13
Place Food – Bring phase	1.02	0.10
Place Non-food – Reach phase	0.97	0.10
Place Non-food – Bring phase	0.94	0.11

## Figure Captions

*Figure 1.* Normalized EMG activity of the mylohyoid muscle during the observation of eating and placing actions performed with food and non-food objects, collapsed across the two phases. Asterisk indicates significant difference between conditions,  $p < .05$  (corrected for multiple comparisons). Error bars indicate standard error.

*Figure 2.* Timecourse of the normalized EMG activity of the mylohyoid muscle during the observation of actions performed with food and non-food objects, collapsed across the two intentions. Dashed vertical line indicates the timepoint of the observed grasp. Error bars indicate standard error.

## Figures

Figure 1

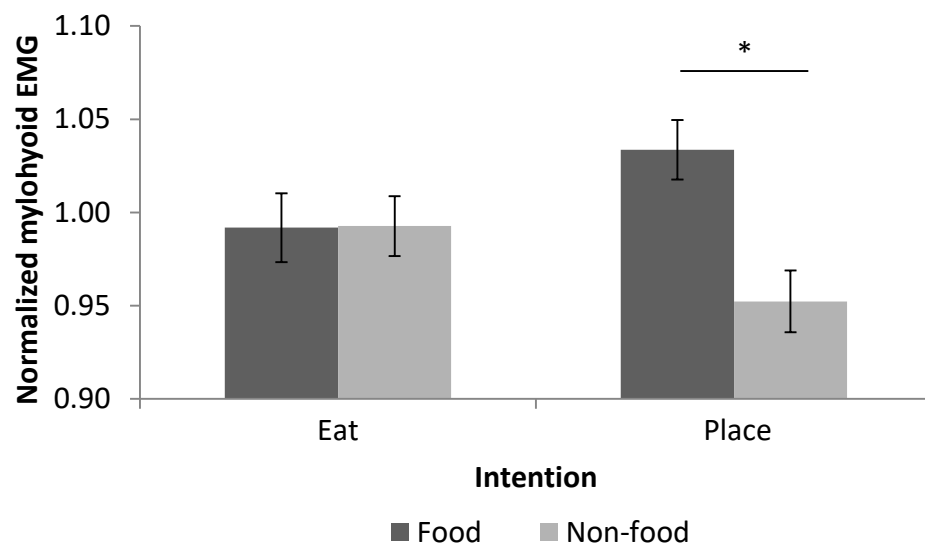


Figure 2

